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Review

The Affinity of Moss Floras of Japan, Taiwan and the Philippines Revisited: Old Problems, New Insight and More Questions[1]

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A review of the floristic affinity of moss floras of Japan, Taiwan and the Philippines is presented. The results show that as many as 50 genera of mosses in Japan do not disperse southward to Taiwan while there are only 28 genera from Taiwan not found in Japan. Japanese moss taxa not present in Taiwan are the arctic and boreal members whereas the Taiwan moss taxa not found in Japan are the Malesian, Himalayan and SW Chinese endemics. A comparison of the floristic affinity of the moss floras of the Philippines and Taiwan reveal the same uneven north/south exchange of moss taxa. 57% of Philippine mosses are not found in Taiwan while a high 64% of Taiwan mosses are not found in the Philippines. The demarcation line between the Taiwan and the Philippine (Luzon) floras is shown to be a strong barrier and be renamed Merrill's Line. Climatic, biological and geological factors causing the differences in species composition and patterns of distribution among the moss floras of Japan, Taiwan and the Philippines are outlined. Lastly, the reported oceanic distribution pattern of mosses from Japan to Taiwan and northern Philippines is also discussed.

Keywords: Japan, Malesia, Merrill's Line, mosses, Philippines, Taiwan, Wallace's Line

Japan, Taiwan and the Philippines are the three island groups in East Asia that have well studied moss flora, each with a modern and updated checklist. By comparing the affinities of the moss floras of Japan, Taiwan and the Philippines, some noteworthy facts and problems in East Asiatic bryogeography can be demonstrated.

At present, the moss flora of Japan has 321 genera and 1183 species (Iwatsuki 1991, 1994). The percentage of species endemism is about 10% (Iwatsuki 2000). The large moss flora of Japan was attributed by Iwatsuki (1994) to the oceanic environment and the long latitudinal expanse the archipelago astride from 25° N (Ryukyu) to 45° N (Hokkaido), thereby giving the country much climatic diversity, high precipitation and a complicated topography, not to mention the contribution made by a large number of active Japanese muscologists in residence.

Taiwan has 278 genera and 835 species (Chiang *et al.* 2001) with a species endemism of 9.6% (Chiang 1998). The island, although having an oceanic climate, lies only between 21° N and

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25° N latitude. The island is bisected at the center by the Tropic of Cancer, which limits its flora to subtropical and temperate taxa.

The Philippine flora has 230 genera and 710 species (Tan & Iwatsuki 1991; Tan *et al.* 2000). The species endemism is a low 5% (Hallingback & Hodgetts 2000). The archipelago, being entirely in the tropics, straddles a north-south distance between 4° N and 21° N latitudes.

Table 1 shows the comparative floristic affinity of Japan, Taiwan, and the Philippines expressed in Kroeber percentage of taxic similarity (%K). ($\%K = C(A+B)/2AB \times 100$, where C is the number of common or shared taxa, A is the number of total taxa in the first area under comparison, and B is the number of total taxa in the second area under comparison.)

Comparing the moss floras of Japan and Taiwan, not counting the endemics, it becomes apparent that the Japanese moss taxa absent in Taiwan are many, at least 50 genera. These are the arctic and boreal genera such as, *Arctoa, Bryhnia, Conostomum, Cyrtomnium, Helodium, Kiaeria, Oreas, Plagiobryum, Plagiopus, Platydicyta, Pleuroziopsis, Podperaea, Pseudobryum, Saelania, Splachnum, Schistostega*, etc. Many of these genera are well represented in continental China at similar high latitudes. Contrastingly, there are only 28 genera found in Taiwan, but not found in Japan. They are either tropical or warm temperate genera, such as *Daltonia, Diaphanodon, Hampeella, Mitthyridium, Papillaria, Pterobryopsis, Spiridens, Trachypodopsis* and *Trismegistia*. A few Himalayan and SW Chinese endemics have reached Taiwan, i.e., *Pseudopleuropus morrisonensis* Takaki and *Horikawaea nitida* Nog., but not Japan. The moss species shared by Taiwan and Japan, but not found in mainland China, were reported to be 230 (Chiang 1998), representing 27% of the total Taiwan mosses, but only 19% of the total Japanese flora.

Seen in this light, the Taiwanese moss flora is closer in affinity to the moss flora of southern China across the Taiwan Strait than to that of Japan, even though Taiwan was allegedly connected to Japan intermittently by a narrow coastal strip of land during the glacial maxima in late Pleistocene when sea level fell to 130 m below the present level (Fergusson 1993). During the interglacial warm climate, the rise of sea level would disrupt the land connection between Taiwan and Japan, resulting in a string of small islands. How this chain of small islands affects the exchange of plant taxa between Taiwan and Japan through the Quaternary is a research area worthy of an in depth study (see Fujii 2001). The earlier claim of Lin & Tsai (1984) for a closer affinity of high mountain mosses of Taiwan and

TABLE 1. Kroeber percentage of taxic similarity (%K) between moss floras of Japan, Taiwan and the Philippines.

Country/Island	Genus		Species	
	Total	Shared (% K)	Total	Shared (% K)
Japan	321		1183	
Taiwan	278	234 (79%)	835	516 (53%)
Philippines	230	147 (55%)	710	217 (25%)

Information: Chiang *et al.* 2001; Iwatsuki 1991; Tan & Iwatsuki 1991; Tan *et al.* 2000.
$\%K = C(A+B)/2AB \times 100$, where C is the number of common or shared taxa, A is the number of total taxa in the first area under comparison, and B is the number of total taxa in the second area under comparison.

Japan in comparison with the affinity of high mountain mosses of Taiwan and northeast China is not supported by the present review. On the other hand, a closer affinity of the moss flora of Japan with that of mainland China than with Taiwan is repeatedly shown by the tropical family, Hookeriaceae (Tan & Lin 1996; Table 2), and the subtropical family, Sematophyllaceae (Tan & Jia 1999; Table 3) at both the generic and species levels. The stronger overall affinity between the moss floras of Taiwan and mainland China over that between Taiwan and Japan would seem to imply that the Pleistocene land connection between Taiwan and Japan was severed prior to the final disruption of the land connection between Taiwan and mainland China in the Holocene.

The same can be said about the floristic comparison between the moss floras of the Philippines and Taiwan. A great majority of the mosses found in Japan and Taiwan, but not in the Philippines, are, undoubtedly, the temperate taxa. Contrastingly, Philippine mosses not reaching Taiwan and Japan are the Malesian endemics and other Southern Hemisphere or Australasian taxa, such as *Dawsonia longifolia* (Bruch & Schimp.) Zant. and *Rhacocarpus alpinus* (Wright) Paris. There are, however, a handful of widespread tropical SE Asiatic mosses (e.g., *Sphagnum junghuhnianum* Dozy & Molk. and *Garovaglia elegans* (Dozy & Molk.) Bosch & Lac.) and Gondwanan mosses (e.g. *Bryum billarderi* Schwägr.) reaching continental China, Taiwan and southern Japan. This group of mosses consists of many lowland forest species.

In summary, mosses common to the Philippines, Taiwan and Japan are: (1) the nearly cosmopolitan or pantropical taxa (e.g., *Bryum argenteum* Hedw., *Funaria hygrometrica* Hedw. and *Ceratodon purpureus* (Hedw.) Brid.), (2) the widespread temperate East Asiatic species (e.g., *Brachymenium nepalense* Hook., *Meteoriella soluta* (Mitt.) Okam. and *Brachythecium buchananii* (Hook.) Jaeg.), (3) the widespread

TABLE 2. Kroeber percentage of taxic similarity (%K) of the Hookeriaceae between Japan, Taiwan and the Philippines. (See Table 1 for the formulation of calculation of %K)

Country/Island	Genus		Species	
	Total	Shared (% K)	Total	Shared (% K)
Japan	5		13	
Mainland China	7	5 (86%)	19	12 (78%)
Taiwan	8	5 (81%)	18	11 (73%)
Philippines	11	5 (73%)	35	8 (42%)

Information: Chiang *et al.* 2001; Iwatsuki 1991; Tan & Lin 1996; Tan & Iwatsuki 1991.

TABLE 3. Kroeber percentage of taxic similarity (%K) of Family Sematophyllaceae between Japan, Taiwan and the Philippines. (See Table 1 for the formulation of calculation of %K)

Country/Island	Genus		Species	
	Total	Shared (% K)	Total	Shared (% K)
Japan	14		42	
Mainland China	16	14 (94%)	45	30 (69%)
Taiwan	18	14 (89%)	38	26 (65%)
Philippines	23	13 (75%)	77	22 (41%)

Information: Chiang *et al.* 2001; Iwatsuki 1991; Tan & Jia 1999; Tan & Iwatsuki 1991.

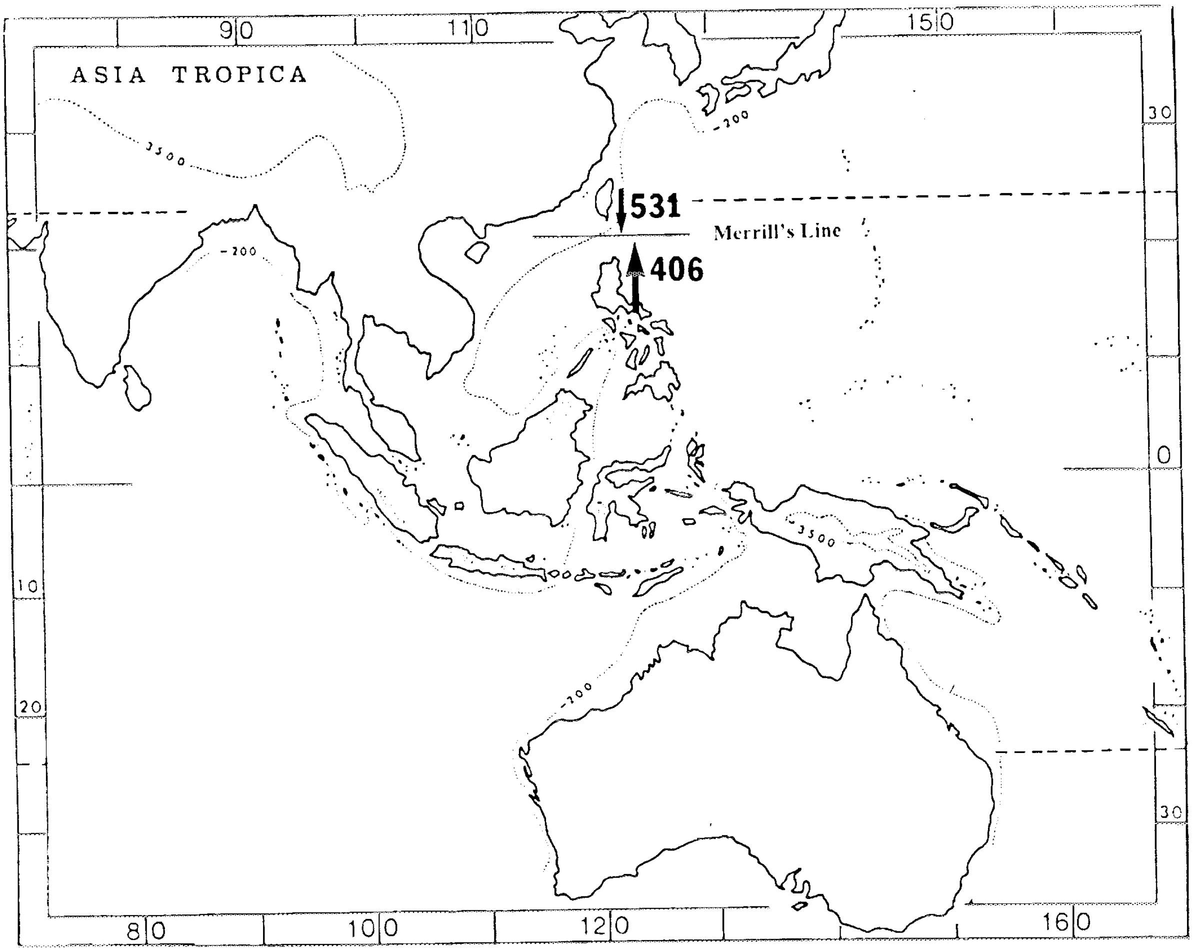
tropical SE Asiatic group (e.g., *Hookeriopsis utacamundiana* (Mont.) Broth., and *Floribundaria floribunda* (Dozy & Molk.) Fleisch.), (4) the anthropogenic, weedy species (e.g., *Barbula indica* (Hook.) Spreng. and *Hyophila involuta* (Hook.) Jaeg.), and perhaps, (5) the ephemeral and "opportunistic" mosses, e.g., species of *Splachnobryum*, *Pleuridium* and *Physcomitrium* (Yip 1999). A recent analysis of correlation between the moss floras of Japan and tropical Peninsular Malaya arrived at a rather similar grouping of their shared taxa (Higuchi 2000).

There have been reports of temperate East Asiatic plants, including the Himalayan taxa, which reached the northern highlands in the Philippines via Taiwan. Because of lack of geologic evidence for a past land connection between Taiwan and northern Philippines during the Tertiary, this suggested route of migration has generated more questions than it has resolved the phytogeographical puzzles.

The similarity and dissimilarity of mosses between the Philippines and Taiwan/Japan have their causes in the Tertiary plate tectonics of SE Asia. At present, the geological evidence is clear about the composite origin of the Philippine archipelago (Hall 1996). For example, the island of Palawan was reported to have been positioned near the coast of China, forming part of a continuous continental shelf with Hainan and Taiwan during the Eocene some 50 million years ago. Because of the opening of the South China Sea in the Oligocene, the asunder Palawan block was pushed to its present location in the Philippine archipelago. The Luzon block also moved north from near the Equator to become positioned south of Taiwan while the Mindanao island group drifted from south of the Equator to its present geographic position at the end of Pleistocene. The geochronological juxtaposition of Taiwan and the Philippines (Luzon) is therefore interpreted to be recent. The time may yet be short for the successful penetration of many Malesian mosses into Taiwan and Ryukyu, in spite of the predominant wind direction of the yearly southeast typhoons that originate in the Pacific Ocean. These typhoons, often devastating northern and central Philippines before hitting Taiwan or landing in Japan, could carry significant numbers of plant diaspores. Lastly, a few enigmatic and widely disjunctive species, such as *Diphyscium chiapense* Norris (Tan 1998), require more collections from the intervening countries before a meaningful phytogeographical statement can be made.

As mentioned above, the narrow Luzon Strait or Bashi Channel between northern Philippines and southern Taiwan, that separates the two biotas, is a strong and filtering barrier to both plant and animal migrations (Map 1). The barrier effect of this natural line of demarcation on the distribution of seed plants in the region has long been noted (Merrill 1926, 1928, van Steenis 1950). Subsequent plant geographers have referred to it informally as the modified Wallace's Line or Merrill-Huxley Line (Wulff 1943, Good 1964). Indeed, for the mosses, the effectiveness of this barrier is more dramatic than that of the better known Wallace's Line that passes between southern Philippines and Halmahera, Borneo and Sulawesi, as well as between Bali and Lombok (Map 1). In recognition of the phytogeographical contribution of Prof. E. D. Merrill who first launched a detailed discussion of the Formosan affinity of the Benguet-Bontoc flora and the botanical alliance between the Philippines and Taiwan (Merrill 1926, 1928), this segment of biotic line of demarcation between Luzon and Taiwan is henceforth to be formally called Merrill's Line.

When van Steenis (1950) discussed the northern demarcation knot (Merrill's Line in this paper) in his delineation of the Malesian floristic region, he reported some 686 genera



Map 1. Location of Merrill's Line between the Philippines and Taiwan. The figure represents the number of moss species that do not cross over Merrill's Line.

of seed plants that do not cross the line. For mosses, which are dispersed mainly by windborne spores, the number of genera crossing the demarcation knot is expectedly higher in percentage, with a total of 176 genera, representing 53% of the combined generic flora of Taiwan and the Philippines. The number of species in common is 304, which translates to 24% of the combined species floras of the two areas. This figure (24%) is lower than the calculated 31% of Malesian species that cross Wallace's Line from both directions (Table 4).

Looking at the situation from another angle, 57% of the Philippine moss species do not cross Merrill's Line to reach southern Taiwan, while 64% of the Taiwan moss species do not cross Merrill's Line to reach the Philippines (Table 4). The apparent direction of dispersal is more from the Philippines to Taiwan than vice versa. This can be explained by the prevailing wind pattern, such as from typhoons, between the two island groups. The absence of extensive temperate habitats in the Philippine mountains may be another reason. The competition for ecological niche between the already established local montane mosses and the new arrival of temperate mosses also helps explain the absence of some temperate Taiwan mosses in the Philippines.

Iwatsuki & Sharp (1968) mapped the range of a number of alleged oceanic moss taxa that are distributed from Japan and Taiwan to Luzon Island of the Philippines. Examples given in the literature are *Oligotrichum aligerum* Mitt.,

TABLE 4. A comparison of the numbers of moss species of regions on both sides of the Merrill's Line and Wallace's Line.

Phytogeographical line	Region	No. of total spp.	No. of common species(%*)	No. of spp. not crossing the Line(%**)	References***
Merrill's Line	Taiwan	835	304 (24%)	531 (64%)	R1
	Philippines	710	304 (24%)	406 (57%)	R2
Wallace's Line	Philippines/Borneo	880	425 (31%)	455 (52%)	R3
	New Guinea/Seram	920	425 (31%)	495 (54%)	R4

* Percentage of number of common species calculated on the basis of 1,241 species of combined Philippine and Taiwan moss floras for the Merrill's Line, and on the basis of 1,375 species of combined Philippine, Bornean, New Guinean and Seram moss floras for the Wallace's Line.

** Percentage of number of species that do not cross the biogeographical line to that of the total species of each moss flora under discussion.

*** R1: Chiang *et al.* (2001).
R2: Tan & Iwatsuki (1991), Tan *et al.* (2000)
R3: Tan & Iwatsuki (1991), Tan *et al.* (2000) for the Philippines; Touw (1978), Enroth (1989), Hyvonen (1989), Menzel & Schultze-Motel (1991), Menzel (1992), Tan (1994) for Borneo.
R4: Akiyama (1991, 1992, 1993, 1996, 1997) for Seram; Schultze-Motel (1963) and list of publications in Koponen *et al.* (1992) for New Guinea.

Fauriella tenuis (Mitt.) Card. and *Bryoxiphium norvegicum* (Brid.) Mitt. ssp. *japonicum* (Berggr.) Löve & Löve. Recent studies have shown that these mosses share only a superficially similar pattern of distribution. In reality, they are of composite origin. In fact, some have subsequently been found on the continent, reaching as far south as Indochina and even Java. For majority of them, the direction of migration into Japan, Taiwan and the Philippines probably took three separate routes at different geologic times. This hypothesis of polytopic origin is supported by the presence of vicarian or closely related species in a number of genera such as *Horikawaea, Holomitrium* and *Rhynchostegiella*, in Taiwan and the Philippines, as well as in Taiwan and Japan. The subsequent extinction of populations on the continent may have resulted in the current artifact pattern of oceanic distribution from Japan to Taiwan and the Philippines.

To date, I do not know of good example of mosses showing a restrictively narrow coastal distribution from Japan to Taiwan and the Philippines. Many of the oceanic, circum North Pacific taxa [e.g. *Rhizomnium nudum* (Britt. & Williams) T. Kop.] that are common in the subalpine zone in Honshu and Hokkaido (Z. Iwatsuki, pers. comm. 2001) reach only Japan or Japan and Taiwan, but not the Philippines. That this direct route of migration by island hopping along the extended East Asiatic coastline is not easy to achieve can be surmised from the prevailing wind direction, the plate tectonic history in the region, and last but not the least, the difficulty for a species to achieve a broad ecological amplitude needed to complete the southward migration from the cold northern coast of Japan, to warm temperate Taiwan, and into the tropical Philippine islands.

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